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Phylogenetic Relationships of the Enigmatic Harpy Fruit Bat, *Harpyionycteris* (Mammalia: Chiroptera: Pteropodidae)

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ABSTRACT

Harpy fruit bats, two closely related species in the genus *Harpyionycteris* (Chiroptera: Pteropodidae), exhibit a suite of unique craniodental traits. For this reason, the affinities of these bats have remained unclear, and most systematists have placed them in a group of their own (Harpyionycterinae Miller, 1907). The multicuspidate pattern of the cheek teeth in *Harpyionycteris* has generated speculation that it may represent an ancestral tribosphenic pattern lost in other pteropodids. In this contribution we propose a phylogenetic placement of *Harpyionycteris* based on parsimony analysis of complete sequences from two coding genes, the nuclear vWF (exon 28) and the mitochondrial cytochrome *b* (cyt-*b*). Both datasets, independently and in combination, strongly support a close relationship between *Harpyionycteris* and *Dobsonia*, as originally proposed by Andersen (1912, *Catalogue of Chiroptera*, British Museum Trustees). In turn, this group nests deeply inside Pteropodidae but it is not closely related to any particular suprageneric clade. Based on other data, we postulate that *Aproteles* also belongs in this group and therefore propose the expansion of Harpyionycterinae to include *Harpyionycteris*, *Aproteles*, and *Dobsonia*. Regarding the dentition, our results strongly reject the tribosphenic hypothesis advanced by some authors. The multicuspidate cheek tooth pattern seen in *Harpyionycteris* appears uniquely derived

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and related to specialized feeding habits and it thus has no direct bearing on the evolution of the typical pteropodid dentition from the tribosphenic pattern of microchiropterans and other mammals.

INTRODUCTION

The systematic position of the Harpy fruit bats (*Harpyionycteris* Thomas, 1896) has been controversial since the original description of the genus. Thomas (1896: 243) described this genus for a single species, *H. whiteheadi*, from the Philippines. Although he associated it with rousettines, to him *Harpyionycteris* was "one of the most isolated of all genera" of Megachiroptera. This assessment was based on craniodental characters exhibited by *Harpyionycteris*, including uniquely multicuspidate cheek teeth (figs. 1, 2). The unusual nature of the skull and dentition subsequently prompted Miller (1907) to place this genus in a separate subfamily, Harpyionycterinae. In his influential monograph on the Megachiroptera, Andersen (1912: 800) followed Miller in recognizing Harpyionycterinae, emphasizing its highly distinct characters:

> Each of the following single characters appears to be absolutely diagnostic: (1) premaxillae, upper incisors, and upper and lower canines strongly proclivous (canines crossing each other at nearly right angles when the jaw is closed); (2) lower canines tricuspidate; (3) molariform teeth multicuspidate; (4) tibia less than one-third of forearm (only slightly longer than foot with claws).

However, Andersen (1912) also explicitly linked *Harpyionycteris* with *Dobsonia* and discussed at length both the characters supporting this perceived association and the features by which *Harpyionycteris* appeared more derived with respect to *Dobsonia*. Several years later, Miller and Hollister (1921) described a second species from Sulawesi, *Harpyionycteris celebensis*. Tate (1951: 4) examined new specimens from both the Philippines and Sulawesi and recognized the two taxa as distinct but he left open the question of whether they deserve the status of species or subspecies, noting that they differ by "extremely slight characters". Subsequent authors have either treated *celebensis* as a subspecies of *whiteheadi* (e.g., Laurie and Hill, 1954; Koopman, 1994) or more commonly as a separate species (e.g., Bergmans and Rozendaal, 1988; Corbet and Hill, 1992; Hill,1983; Koopman, 1993; Peterson and Fenton,1970; Simmons, 2005), although often with some reservations.

Tate (1951) disregarded the association of *Harpyionycteris* and *Dobsonia* proposed by Andersen (1912), and he considered the dental characters of *Harpyionycteris* to be derived relative to those of other megachiropterans. By contrast, Slaughter (1970) suggested that *Harpyionycteris* represents a prototype from which all megachiropteran dentitions can be derived by simplification of the cusp pattern. To Slaughter (1970), the multicuspidate condition seen in *Harpyionycteris* could be interpreted as a retention of a tribosphenic pattern seen in microchiropterans and other mammals. This point of view was rejected by Hill and Beckon (1978), who supported the hypothesis advanced by Andersen (1912) regarding the origin of the multicuspidate cheek teeth of *Harpyionycteris*. The typical cusp pattern of a postcanine tooth in Megachiroptera consists of a median groove that separates two ridges, medial and lateral, each of which tapers to a point rostrally to form medial and lateral main cusps. In several megachiropterans (e.g., in *Pteralopex* and *Pteropus* species of the *pselaphon* species group; Andersen, 1912) the lateral and medial ridges are each subdivided into more than one cusp, although the main rostral cusp remains clearly distinct. To Andersen (1912) and Hill and Beckon (1978), the multicuspidate condition of *Harpyionycteris* is the result of extreme subdivision of the lateral and medial ridges, and reduction of the main cusp so that all cusps are essentially subequal. That is, the multicuspidate condition of the cheek teeth, as well as other dental traits in *Harpyionycteris*, are considered derived.

Authors proposing formal classifications of megachiropterans have generally accepted Miller's (1907) segregation of *Harpyionycteris* in a suprageneric taxon of its own. Koopman and Jones (1970) placed Harpyionycterini within Pteropodinae, as did McKenna and Bell (1997) and Koopman (1994), while Corbet

and Hill (1992) and Bergmans (1997) recognized Harpyionycterinae Miller, 1907 as distinct at the subfamily level. Moreover, von Schultz (1970) elevated the taxon to family level on the basis of characters of the digestive tract.

Harpyionycteris has been included in two previous phylogenetic studies. Springer et al. (1995) and Romagnoli and Springer (2000) used groupings derived from molecular data to constrain searches based on a morphological matrix of 36 characters scored for 36 genera (*Harpyionycteris* was scored for the morphological data only). Both studies recovered *Harpyionycteris* as sister to *Dobsonia* within a larger clade of pteropodine bats, thus supporting Andersen's (1912) treatment. However, this result was not unexpected because the morphological matrix used by Springer et al. (1995) was based entirely on Andersen's (1912) key. The small number of characters, low character-to-taxon ratio, and the uncertainty that inevitably results from use of supraspecific terminals limited the resolving power and character support in Springer et al.'s (1995) study. The problem of placing *Harpyionycteris* in the megachiropteran tree clearly requires further study. Understanding the phylogenetic position of *Harpyionycteris* will also clarify attendant problems of character evolution in this form, particularly the derived versus primitive condition of its dentition, which is the most distinct found in megabats.

In the present study, we report the results of a parsimony analysis of one nuclear and one mitochondrial gene sampled in Philippine *Harpyionycteris* and representatives of all other major clades of megabats. Our results support Andersen's (1912) vision of relationships and indicate the need for an important taxonomic rearrangement of several megachiropteran genera to accommodate the recovered relationships. The polarity of the complex dental features seen in *Harpyionycteris* is also discussed.

METHODS

Taxa

We included members of each major clade (subfamily or tribe) of Megachiroptera in our analyses in order to test the proposed affinities of *Harpyionycteris*. Based on the latest estimate of megabat higher level relationships (Giannini and Simmons, 2005), we included two Nyctimeninae (*Nyctimene albiventer* and *N. vizcaccia*), two Cynopterinae (*Cynopterus sphinx* and *Ptenochirus jagori*), three Dobsoniini (*Dobsonia minor*, *D. moluccensis*, and *D. inermis*), two Pteropodini (*Pteropus hypomelanus* and *P. tonganus*), two Rousettini (*Rousettus aegyptiacus* and *R. amplexicaudatus*), two Myonycterini (*Myonycteris torquata* and *Megaloglossus woermanni*), two Epomophorini (*Epomophorus wahlbergi* and *Epomops franqueti*), and two macroglossine megabats, *Melonycteris fardoulisi* and *Macroglossus minimus*. Two individuals of *Harpyionycteris whiteheadi* from Mindanao, Philippines, were included in our analyses (see appendix 1). To root our megabat subtree, and therefore to allow for testing character polarity within megabats, we included several microbats as outgroups. Specifically, we included two yangochiropterans (*Artibeus jamaicensis* and *Plecotus auritus*) and two yinochiropterans (*Rhinopoma hardwickei* and *Rhinolophus creaghi*), which were selected on the basis of sequence availability (see appendix 1). An additional analysis was done with *Rhinolophus pumilus* in place of *R. creaghi* (see below).

The ingroup taxonomic sampling, though not intended to cover the full diversity of megabats, includes most key suprageneric megabat clades, and certainly includes all relevant groups with which *Harpyionycteris* has variously been associated throughout its systematic history. Three hypotheses can be tested using our taxonomic sample: segregation of *Harpyionycteris* in a group of its own (sustained by most authors, including Thomas, 1896; Miller, 1907; Tate, 1951; Koopman and Jones, 1970; Koopman, 1994; Bergmans, 1997); association of *Harpyionycteris* with rousettines (Thomas, 1896); and association of *Harypionycteris* with dobsoniines (Andersen, 1912; Springer et al., 1995). In particular, the first hypothesis would be rejected if *Harpyionycteris* is found to nest within any of the suprageneric groups listed above.

Sequences

We used newly generated sequences as well as published sequences. Total DNA was

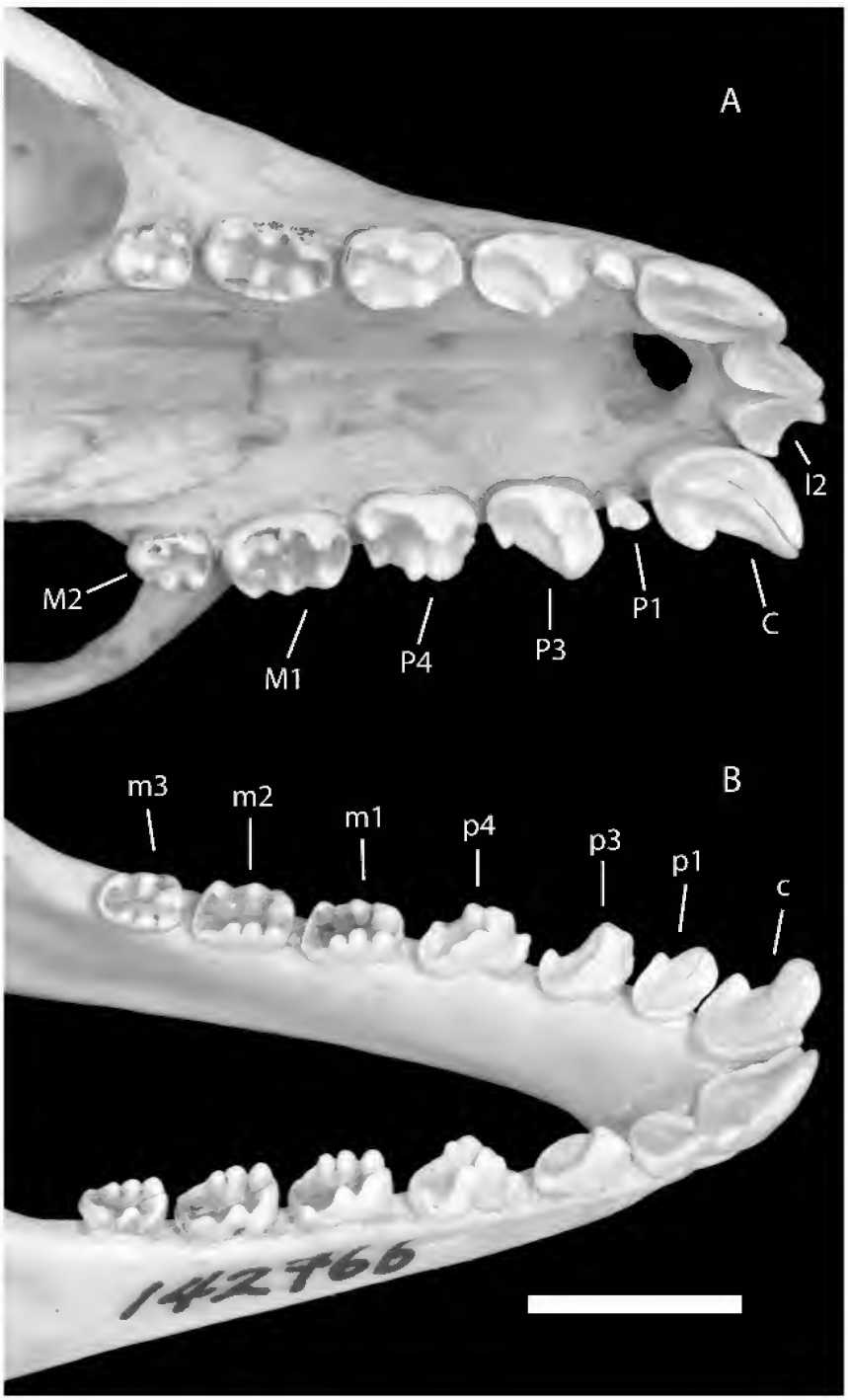

Fig. 1. *Harpyionycteris whiteheadi* FMNH 142766, view of the upper (**A**) and lower (**B**) tooth rows. Abbreviations: c, lower canine; C, upper canine; I2, second upper incisor; m1, first lower molar; M1, first upper molar; m2, second lower molar; M2, second upper molar; m3, third lower molar; p1, first lower premolar; P1, first upper premolar; p3, third lower premolar; P3, third upper premolar; p4, fourth lower premolar; P4, fourth upper premolar. Homology of teeth according to Andersen (1912). Scale = 5 mm.

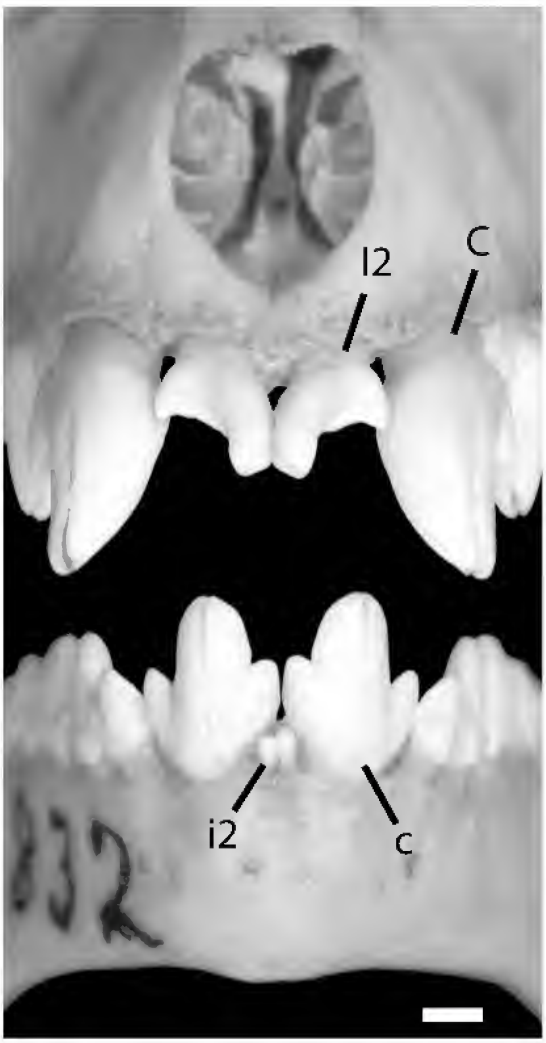

Fig. 2. *Harpyionycteris celebensis* AMNH 196437, rostral view of the apex of the skull and mental view of the mandible. Abbreviations: c, lower canine; C, upper canine; i2, lower second incisor; I2, upper second incisor. Homology of teeth according to Andersen (1912). Scale = 1 mm.

obtained from preserved tissue samples (see voucher list in appendix 1) with the DNeasy tissue kit (QIAGEN). Sequences of two coding genes, one nuclear (1231 bp of exon 28 of the von Willerbrand factor gene) and one mitochondrial (1140 bp of the cyt-*b*), were generated using standard methods. PCR amplification was carried out using previously published primers (vWF: Porter et al., 1996; cytochrome *b*: Bastian et al., 2002). In order to obtain both forward and reverse sequences for each gene region, internal primers were used for sequencing in addition to the PCR primers (sequences available upon request). All sequences were obtained with an automated ABI 3730XL sequencer. Sequence editing and prealignment were done with the Sequencher 4.2 software (Gene Codes).

Accession numbers for the new sequences are DQ445684-714. Voucher information is provided in appendix 1. In addition, we used published sequences of *Artibeus jamaicensis* (AF447542, NC_002009), *Cynopterus sphinx* (AY629004), *Dobsonia moluccensis* (U31209, AF144064), *Epomophorus wahlbergi* (AF044642), *Epomops franqueti* (AF044639), *Myonycteris torquata* (AF044650), *Nyctimene albiventer* (AF447549, DQ14264), *Plecotus auritus* (AB079840, AB085734), *Pteropus hypomelanus* (AF203777, AB062472), *Pteropus tonganus* (AF044656), *Rhinopoma hardwickei* (AF447551, AY056462), *Rhinolophus creaghi* (AF447546, DQ178986), *Rhinolophus pumilus* (NC_005434), and *Rousettus amplexicaudatus* (AY057836, AB046329). Although for some species more than one sample was available, only one was included in the final analysis. The aligned dataset is provided at ftp://ftp.amnh.org/pub/group/mammalogy/downloads/.

Phylogenetic Analyses

Aligned sequences of the vWF and cyt-*b* genes were submitted to parsimony analysis both individually and in combination. In the cyt-*b* analysis, the outgroup *Rhinolophus creaghi* was identified as the cause of a collapse in the backbone of the tree due to its incomplete sequence; as a consequence, it was replaced by the complete sequence of its close relative *R. pumilus* and the problem was eliminated. However, sequences of the vWF are not available for *R. pumilus*, so in the combined analysis we used the complete vWF and the partial cyt-*b* sequences of *Rhinolophus creaghi*, which did not affect resolution. The tree search strategy consisted of 500 replicates of random addition sequences of taxa each followed by tree bisection reconnection branch swapping (TBR). An additional round of TBR was done on all optimal trees obtained. Clade support was estimated using

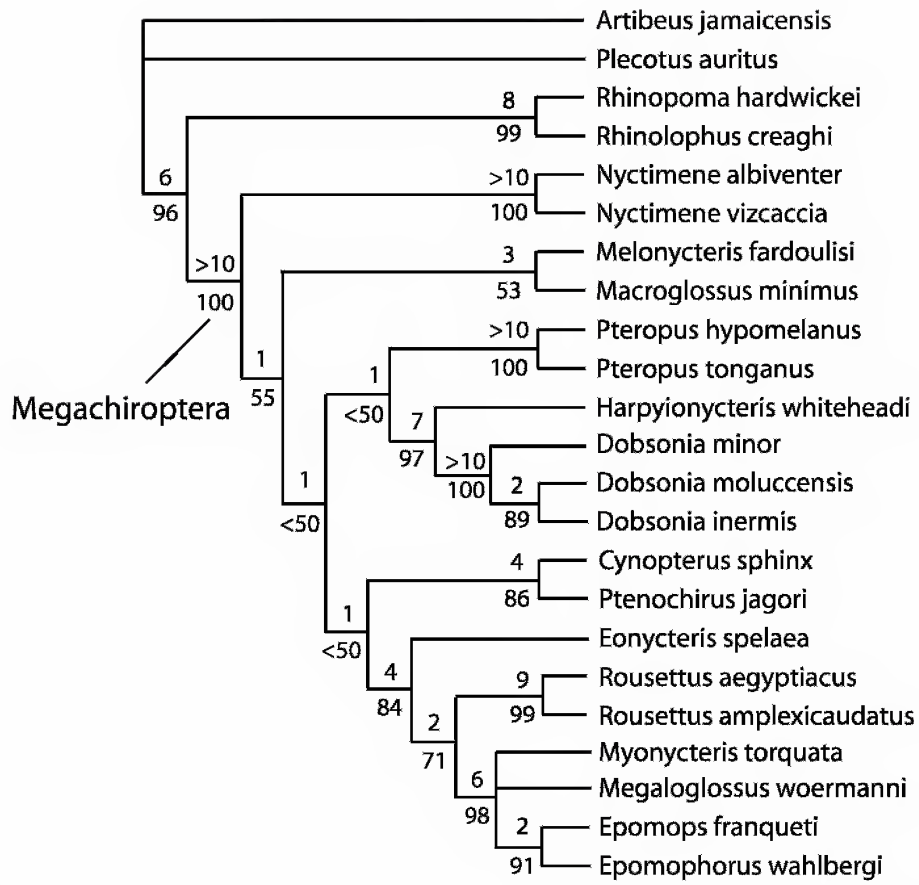

Fig. 3. Results of parsimony analysis using the vWF gene. Strict consensus of two trees of 688 steps. Numbers above branches are Bremer support values. Numbers below branches are jackknife frequencies (cutoff value = 50%).

both Bremer values (Bremer, 1994) and character resampling (Goloboff et al., 2003). For the first method, we followed Giannini and Bertelli (2004). Specifically, we implemented an incremental strategy for obtaining suboptimal trees in successive stages, saving up to 2000 suboptimals in each stage. We first searched for suboptimal trees 1 step longer than the optimal tree length, next saving suboptimals up to 2, 3, 4, 5, 6, 7, 8, 9, and 10 steps longer than the optimal trees. Second, the resampling technique used was a version of the jackknife developed by Goloboff et al. (2003). Group frequency (based on unbiased symmetric resampling) was calculated on the basis of 5000 replications. All analyses were executed in TNT (Goloboff et al., 2004).

RESULTS

The parsimony analysis using the vWF gene resulted in two optimal trees of 688 steps (CI = 56, RI = 0.61). Bremer values were calculated using a sample of 8932 trees up to 10 steps longer than the optimal trees sampled incrementally (see Methods: Phylofgenetic Analyses). In the strict consensus topology (fig. 3), outgroup relationships were as expected (yinochiropteran terminals grouped together, as did yangochiropterans), and Megachiroptera was recovered as a monophyletic group with high support (Bremer support, BS > 10; jackknife frequency, JF = 100). Within Megachiroptera, successive sister groups were Nyctimeninae, a macroglossine clade formed by *Melonycteris*

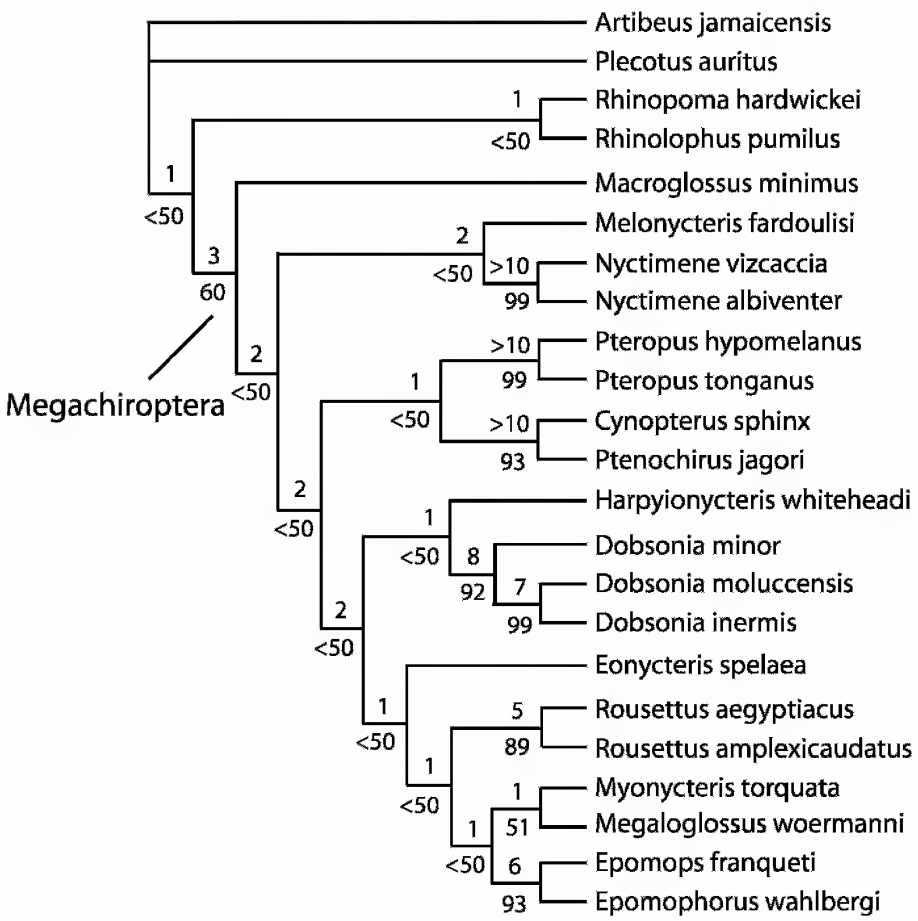

Fig. 4. Results of parsimony analyses using the cyt-*b* gene. Single optimal tree of 1916 steps. Numbers above branches are Bremer support values. Numbers below branches are jackknife frequencies (cutoff value = 50%).

and *Macroglossus*, a *Pteropus* clade sister to *Harpyionycteris* + *Dobsonia*, Cynopterinae, and "clade C" of rousettines, myonycterines, and epomophorines found in previous analyses by Giannini and Simmons (2003, 2005). The latter was composed of *Eonycteris*, *Rousettus*, Myonycterini (*Myonycteris* + *Megaloglossus*), and Epomophorini (*Epomops* + *Epomophorus*). Support values along the backbone of the megabat subtree (linking subfamilies or tribes) were minimal (BS = 1, JF < 50) except for clade C (BS = 4, JF = 84), whereas most of the suprageneric groups were reasonably supported. A sister-group relationship between *Harpyionycteris* and *Dobsonia* was particularly well supported (BS = 7, JF = 97), as was the monophyly of *Dobsonia* (BS > 10, JF = 100).

Parsimony analysis of the cyt-*b* gene resulted in a single optimal tree (fig. 4) of 1916 steps (CI = 0.42, RI = 0.35). Bremer values were calculated from an incremental sample of 10,670 suboptimal trees. This analysis recovered Megachiroptera as monophyletic but the support level was low (BS = 2, JF < 50). Successive sister groups were *Macroglossus*, *Nyctimene* + *Melonycteris*, Pteropodini + Cynopterinae, *Harpyionycteris* + *Dobsonia*, and the clade C. Support values were minimal along the backbone (BS = 1, JF < 50) and slightly higher in the suprageneric groups. *Harpyionycteris* + *Dobsonia* was recovered but support was minimal (BS = 1, JF < 50).

The combined analysis of vWF + cyt-*b* resulted in two trees (strict consensus in fig. 5) at 2507 steps (CI = 0.42, RI = 0.42).

Using the same search strategy, just 519 suboptimal trees were found that were up to 10 steps longer than the optimal trees. Support in resolved backbone clades was low to moderately high ($1 \leq BS \leq 6$, $50 \leq JF \leq 81$), as were all suprageneric groups recovered ($3 \leq BS \leq 10$ for most groups, but for some $BS > 10$, and most $JF > 50$). Successive sister groups in the optimal tree were Nyctimeninae, a macroglossine clade formed by *Melonycteris* and *Macroglossus*, and a trichotomy formed by Pteropodini, Cynopterinae, and a clade containing the remaining groups. The last clade included *Harpyionycteris* + *Dobsonia*, and the clade C. The clade formed by *Harpyionycteris* + *Dobsonia* was highly supported ($BS > 10$, $JF = 89$).

DISCUSSION

Results based on both separate and combined analyses of our two genes strongly suggest a close phylogenetic relationship between *Harpyionycteris* and *Dobsonia*, as initially suggested by Andersen (1912) and later recovered by Springer et al. (1995) based on morphological evidence. The vWF analysis also suggests, albeit weakly, that *Dobsonia* + *Harpyionycteris* may be linked to pteropodines as found by Springer et al. (1995). However, the cyt-*b* signal recovered a clade formed by pteropodines + cynopterines. In the combined analysis, the conflicting signals caused a polytomy involving pteropodines and cynopterines. *Harpyionycteris* + *Dobsonia* formed a separate group in the next resolved node up in the tree, sister to clade C (fig. 5). Giannini and Simmons (2005) found that dobsoniine bats (*Aproteles* and *Dobsonia*) form a clade not closely associated with any particular suprageneric clade (Giannini and Simmons, 2005: fig. 7).

Andersen (1912) established a solid argument for the relationship between *Harpyionycteris* and the other megachiropterans known to him, specifically highlighting a phylogenetic link to *Dobsonia*. He did so on the basis of putatively derived traits shared between *Dobsonia* and *Harpyionycteris*, without losing sight of the overwhelmingly distinct craniodental features that make *Harpyionycteris* so easily diagnosable. For instance, he (1913: 804) noted that "If the extremity of the rostrum and mandible of the *Harpyionycteris* skull were removed from view, it would be difficult to point out any cranial character of generic importance to separate it from *Dobsonia* ...".

Andersen (1912) identified other taxonomically important similarities between the two genera, including: form of the braincase and postdental palate, position of all cranial foramina, deflection of basicranial axis, similar dental formulae (first upper premolar lost in *Dobsonia*), loss of the first upper and lower incisor, and left and right lower canines displaced rostromedially to nearly contacting each other. As expected, a phylogenetic analysis based on some of Andersen's characters recovered this association (Springer et al., 1995). Based on one nuclear and one mitochondrial gene, we independently recovered a well-supported sister group relationship between *Harpyionycteris* and *Dobsonia*.

We further postulate that *Aproteles* is also a member of the *Harpyionycteris* + *Dobsonia* group. In the original description of *Aproteles*, Menzies (1977) recognized its cranial and external resemblance to *Dobsonia*. Moreover, a close association of *Aproteles* and *Dobsonia* has been supported in all previous phylogenetic analyses in which *Aproteles* was included (Colgan and da Costa, 2002; Giannini and Simmons, 2003, 2005; Jones et al., 2002; Kirsch et al., 1995). In the present study we did not have access to tissue samples of *Aproteles*, and the genes we sequenced were not previously reported for this form, so we cannot resolve relationships among the three genera on the basis of our current molecular data. However, *Aproteles* undoubtely shares more derived morphological traits with *Dobsonia* (most notably, the bare back) than with *Harpyionycteris*. We predict that future studies including all three genera will demonstrate a sister-group relationship between *Dobsonia* and *Aproteles*, with *Harpyionycteris* as sister to that clade.

The recognition that *Harpyionycteris*, *Dobsonia*, and *Aproteles* belong in a monophyletic group to the exclusion of other genera requires changes in the higher level classification of megabats. We recommend that Harpy-

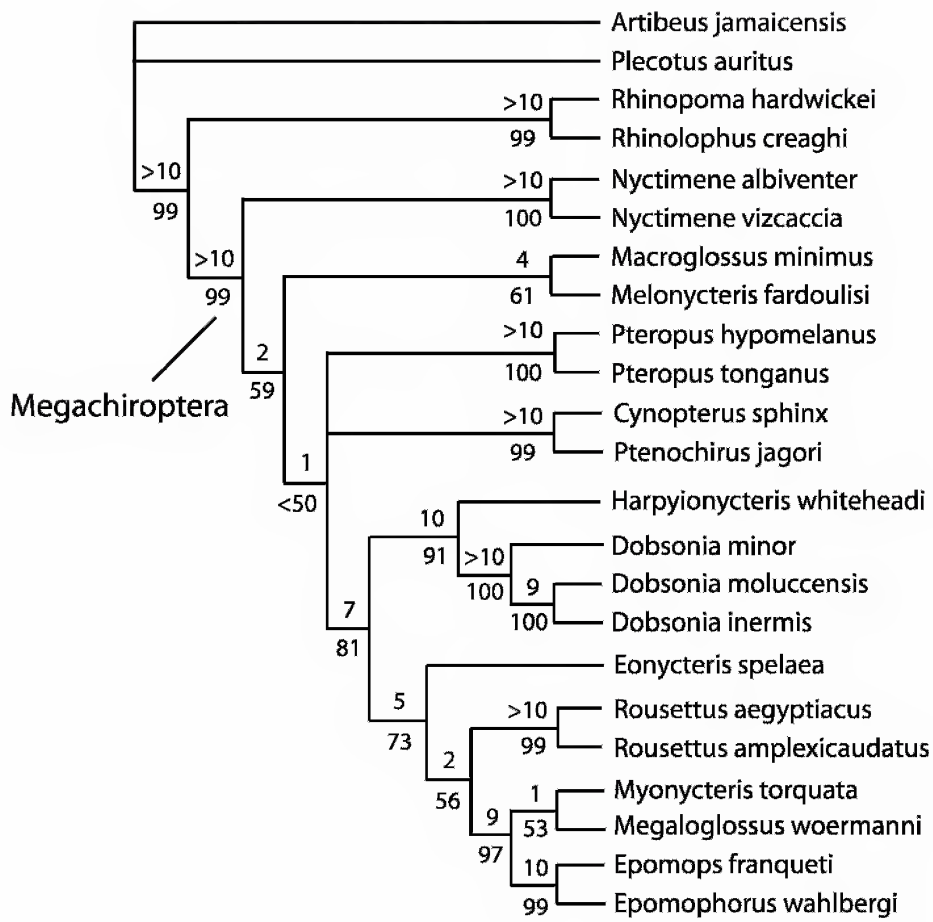

Fig. 5. Results of the parsimony analyses combining vWF and cyt-*b* sequences. Strict consensus of two optimal trees of 2507 steps. Numbers above branches are Bremer support values. Numbers below branches are jackknife frequencies (cutoff value = 50%).

ionycterinae Miller, 1907 be expanded to include *Harpyionycteris* Thomas, 1896, *Dobsonia* Palmer, 1898, and *Aproteles* Menzies, 1977. This arrangement differs from Bergmans (1997) in that the tribe Dobsoniini Andersen, 1912, formed by *Dobsonia* and *Aproteles*, is transferred from Rousettinae Andersen, 1912 to Harpyionycterinae, the oldest name available for this new group. Maintaining Dobsoniini as a tribe within Harpyionycterinae requires recognizing the tribe Harpyionycterini, which seems superfluous for such a small group.

Members of the newly defined Harpyionycterinae are distributed in the center of the Australasian region. Andersen (1912: 803) made a strong biogeographical statement based on his association of *Harpyionycteris* with *Dobsonia*: "So evident is the intimate phylogenetic connection between these two genera that *Harpyionycteris* may be said, almost with certainty, to be the peculiarly modified Philippine representative of the Austro-Malayan *Dobsonia*."

The subsequent discovery of *Harpyionycteris* in Sulawesi (Miller and Hollister, 1921) substantiated the biogeographical link between the two genera. While *Harpyionycteris* is a Philippine/Wallacean genus with its two species separated by the Wallace's line, *Dobsonia* is essentially Wallacean/Papuan. However, 3 of the 14 currently recognized species of *Dobsonia* (Simmons, 2005) narrowly escape the boundaries of these two regions

combined (*Dobsonia chapmani* in the Philippines, *D. peronii* in Bali, and *D. magna* in Cape York Peninsula, Australia). As far as is known, the recently discovered *Aproteles* is Papuan. Overlap exists in the distribution of the three harpyionycterine genera, but it is limited to few instances involving few species at a time. *Aproteles* and two species of *Dobsonia* (*D. magna* and *D. minor*) are sympatric in Papua New Guinea, but probably *D. minor* and *A. bulmerae* are not syntopic as they differ in their elevational range; that is, they are lowland and highland species, respectively, whereas *D. magna* is widespread (Flannery, 1995). Harpy fruit bats formerly assigned to *Harpyionycteris whiteheadi negrosensis* Peterson and Fenton, 1970 (not currently recognized as a separate subspecies; Simmons, 2005) and *D. chapmani* both occur in Negros Island (the Philippines). *Harpyionycteris celebensis* coexists with three species of *Dobsonia* in Sulawesi (*D. crenulata*, *D. exoleta*, and *D. minor*).

The relationships recovered in our analyses imply that the unusual multicuspidate molars of *Harpyionycteris* cannot possibly represent the retention of an ancestral tribosphenic pattern. Therefore, the most plausible explanation for the cusp pattern of *Harpyionycteris* is the one proposed by Andersen (1912): the multiple cusps of *Harpyionycteris* are derived from repeated subdivisions of the simple cusp pattern typical of pteropodids (fig. 1). The strong dentition of *Harpyionycteris* might represent a dietary specialization not shared with other megachiropterans. Before anything was known about the diet of *Harpyionycteris*, Peterson and Fenton (1970: 8) speculated that "it is a fruit eater, perhaps adapted for a particular type of tough-textured fruit for which the multicuspid teeth would be advantageous in extracting the juice". This hypothesis has been confirmed to a large extent, at least in the Philippines. *Harpyionycteris* principally occurs in mid-elevation forests (Heaney et al., 1989, 1998) were it feeds on the hard-seeded, tough-skinned fruits with fibrous mesocarp of a locally abundant vine (*Freycinetia*, Pandanaceae; Heaney et al., 1998, 1999; Utzurrum, 1995). Although *Harpyionycteris* also feeds on *Ficus* as do all other Philippine megachiropterans, no other fruit bat appears to consume *Freycinetia* fruits (Utzurrum, 1995).

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REFERENCES

Andersen, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. Volume I: Megachiroptera. London: Trustees British Museum (Natural History).

Bastian Jr., S.T., K. Tanak, R.V.P. Anunciado, N.G. Natural, A.C. Sumalde, and T. Namikawa. 2002. Evolutionary relationships of flying foxes (genus *Pteropus*) in the Philippines inferred from DNA sequences of cytochrome *b* gene. Biochemical Genetics 40: 101–116.

Bergmans, W. 1997. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899, and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. Beaufortia 47: 11–90.

Bergmans, W., and F.G. Rozendaal. 1988. Notes on the collection of fruit bats from Sulawesi and some off-lying islands (Mammalia, Megachiroptera). Zoologische Verhandelingen 248: 1–74.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Colgan, D.J., and P. da Costa. 2002. Megachiropteran evolution studied with 12S rDNA and *c*-mos DNA sequences. Journal of Mammalian Evolution 9: 3–22.

Corbet, G.B., and J.E. Hill. 1992. Mammals of the Indomalayan region: a systematic review. Oxford: Oxford University Press.

Giannini, N.P., and S. Bertelli. 2004. A phylogeny of extant penguins based on integumentary characters. Auk 121: 422–434.

Giannini, N.P., and N.B. Simmons. 2003. A phylogeny of megachiropteran bats (Mammalia: Chiroptera: Pteropodidae) based on direct optimization analysis of one nuclear and four mitochondrial genes. Cladistics 19: 496–511.

Giannini, N.P., and N.B. Simmons. 2005. Conflict and congruence in a combined DNA-morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). Cladistics 21: 411–437.

Goloboff, P.A., J.S. Farris, M. Källersjö, B. Oxelman, M. Ramírez, and C. Szumik. 2003. Improvements to resampling measures of group support. Cladistics 19: 324–332.

Goloboff, P.A., J.S. Farris, and K. Nixon. 2004. T.N.T.: tree analysis using new technologies. Program and documentation. Available at www.cladistics.org.

Hill, J.E. 1983. Bats (Mammalia: Chiroptera) from Indo-Australia. Bulletin of the British Museum (Natural History) Zoology 45: 103–208.

Hill, J.E., and W.N. Beckon. 1978. A new species of *Pteralopex* Thomas, 1888 (Chiroptera: Pteropodidae) from the Fiji Islands. Bulletin of the British Museum (Natural History) Zoology 34: 65–82.

Jones, K.E., A. Purvis, A. MacLarnon, O.R.P. Bininda-Emonds, and N.B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). Biological Reviews 77: 223–259.

Kirsch, J.A., T.F. Flannery, M.S. Springer, and F.-J. Lapointe. 1995. Phylogeny of the Pteropodidae (Mammalia: Chiroptera) based on DNA hybridization with evidence of bat monophyly. Australian Journal of Zoology 43: 395–428.

Koopman, K.F. 1993. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 2nd ed.: 137–241. Washington, D.C.: Smithsonian Institution Press.

Koopman, K.F. 1994. Chiroptera systematics: handbook of zoology [vol. 8, part 60], Mammalia. New York: Walter de Gruyter.

Koopman, K.F., and J.K. Jones, Jr. 1970. Classification of bats. *In* B.H. Slaughter and D.W. Walton (editors), About bats: 22–28. Dallas: Southern Methodist University Press.

Laurie, E.M.O., and J.E. Hill. 1954. List of land mammals of New Guinea, Celebes and adjacent islands 1758–1952. London: British Museum (Natural History).

McKenna, M.C., and S.K. Bell. 1997. Classification of mammals above the species level. New York: Columbia University Press.

Menzies, J.I. 1977. Fossil and subfossil bats from the mountains of New Guinea. Australian Journal of Zoology 25: 329–336.

Miller, G.S., Jr. 1907. The families and genera of bats. Bulletin of the United States National Museum 57: 1–282.

Miller, G.S., Jr., and N. Hollister. 1921. Twenty new mammals collected by H. Raven in Celebes. Proceedings of the Biological Society of Washington 34: 93–104.

Palmer, T.S. 1898. Random notes on the nomenclature of Chiroptera. Proceedings of the Biological Society of Washington 12: 109–114.

Peterson, R.L., and M.B. Fenton. 1970. Variation in the bats of the genus *Harpyionycteris*, with the description of a new race. Royal Ontario Museum Life Sciences Occasional Papers, Royal Ontario Museum 17: 1–15.

Porter, C.A., M. Goodman, and M.J. Stanhope. 1996. Evidence on mammalian phylogeny from sequences of exon 28 of the von Willerbrand factor gene. Molecular Phylogenetics and Evolution 5: 89–101.

Romagnoli, M.L., and M.S. Springer. 2000. Evolutionary relationships among Old World fruitbats (Megachiroptera: Pteropodidae) based on 12S rRNA, tRNA valine and 16S rRNA gene sequences. Journal of Mammalian Evolution 7: 259–284.

Schultz, S. von. 1970. Einige Bemerkungen zum Bau des Verdauungstraktes und der systematischen Stellung des Spitzzahnflughundes, *Harpyionycteris whiteheadi* Thomas, 1896 (Megachiroptera). Zeitschrift für Säugetierkunde 35: 81–88.

Simmons, N.B. 2005. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 3rd ed.: 312–529. Washington D.C.: Smithsonian Institution Press.

Slaughter, B.H. 1970. Evolutionary trends in chiropteran dentitions. *In* B.H. Slaughter and W.D. Walton (editors), About bats: 51–83. Dallas: Southern Methodist University Press.

Springer, M.S., L.J. Hollar, and J.A.W. Kirsch. 1995. Phylogeny, molecules versus morphology, and rates of character evolution among fruit bats (Chiroptera: Megachiroptera). Australian Journal of Zoology 43: 557–582.

Tate, G.H.H. 1951. *Harpyionycteris*, a genus of rare fruit bats. American Museum Novitates 1522: 1–9.

Thomas, O. 1896. Mammals from Celebes, Borneo, and the Philippines recently received at the British Museum. Annals and Magazine of Natural History (6)18: 241–250.

APPENDIX 1

GenBank Accession Numbers and Voucher Information

Abbreviations of Institutions: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; AMCC, Ambrose Monell Cryo Collection (AMNH); MVZ, Museum of Vertebrate Zoology, University of California, Berkeley. Other abbreviations refer to collector's catalog.

Species	Voucher	Tissue ID	vWF	cyt *b*	Locality
Cynopterus sphinx	AMNH 274354	AMCC 101688	DQ445697	DQ445703	Vietnam, Ha Giang Province, Vi Xuyen District, Cao Bo Commune, Mt Tay Con Linh II
Dobsonia inermis	PRS 2771	AMCC 124428	DQ445686	DQ445704	Solomon Islands, Western Prov., New Georgia Group, Vonavona Lagoon
Dobsonia minor	MVZ 140208	MVZ 140208	DQ445701	DQ445705	Papua New Guinea, Madang Prov., Madang
Eonycteris spelaea	MVZ 176480	MVZ 176480	DQ445685		China, Yunnan Province
Eonycteris spelaea	MVZ 176487	MVZ 176487	DQ445684		China, Yunnan Province
Epomophorus wahlbergi	AMNH 117336	JCK 4820	DQ445691	DQ445706	Mozambique, Zambezia, Mt. Namuli
Epomops franqueti	AMNH 238356	AMCC 109070	DQ445692	DQ445707	Central African Republic, Sangha, Dzanga-Sangha
Harpyionycteris whiteheadi	FMNH 146646	LRH 4811	DQ445690	DQ445708	Philippines, Mindanao, Bukidnon Prov., Mount Kitanglad Range
Harpyionycteris whiteheadi	FMNH 146650	LRH 4866	DQ445689	DQ445709	Philippines, Mindanao, Bukidnon Prov., Mount Kitanglad Range
Macroglossus minimus	CEF 800	AMCC 124283	DQ445693		Solomon Islands, Western Province, New Georgia Group, Vella Lavella Island
Megaloglossus woermanni	AMNH 268358	AMCC 109064	DQ445702	DQ445710	Central African Republic, Sangha, Dzanga-Sangha
Melonycteris fardoulisi	PRS 2653	AMCC 124279	DQ445699		Solomon Islands, Western Prov., New Georgia Group, Vella Lavella Island
Myonycteris torquata	AMNH 268362	AMCC 109058	DQ445700		Central African Republic, Sangha, Dzanga-Sangha
Nyctimene vizcaccia	PRS 2636	AMCC 124208	DQ445698	DQ445711	Solomon Islands, Western Prov., New Georgia Group, Vella Lavella Island
Ptenochirus jagori	FMNH 175395	LRH 6700	DQ445696	DQ445712	Philippines, Luzon, Kalinga Prov., Balbalan Munic., Balbalasang
Pteropus hypomelanus	Uncataloged	P 4447	DQ445687		Captivity Lubee Foundation
Pteropus tonganus	AMNH 272873	AMCC 124962	DQ445695		Tonga
Rousettus aegyptiacus	AMNH 117386	JCK 4960	DQ445688	DQ445713	Mozambique, Zambezia, Mt. Namuli
Rousettus aegyptiacus	AMNH 117335	JCK 4821	DQ445694	DQ445714	Mozambique, Zambezia, Mt. Namuli